

COMMUNITY AND ECOSYSTEM ECOLOGY

Factors Altering the Temporal and Within-Plant Distribution of Coccinellids in Corn and Their Impact on Potential Intra-guild Predation

FRED R. MUSSER¹ AND ANTHONY M. SHELTONDepartment of Entomology, Cornell University, New York State Agricultural Experiment Station,
630 W. North Street, Geneva, NY 14456

Environ. Entomol. 32(3): 575–583 (2003)

ABSTRACT In New York, the primary coccinellid in corn and sweet corn (*Zea mays*, L.) has historically been *Coleomegilla maculata* (DeGeer). However, *Harmonia axyridis* (Pallas) has also been observed the last few years. The objectives of this study were to document the level of establishment of both species in corn and sweet corn and to understand their interactions. The temporal and within-plant distributions of all coccinellids were recorded for 3 yr. The results indicated that *H. axyridis* and *C. maculata* were the only abundant coccinellids in corn and sweet corn, with adults and larvae of both species having distinct temporal and within-plant distributions. *C. maculata* adults were found earlier in the season and lower on the plant than *H. axyridis* adults. Larvae of both species were often found at the same time and were lower on the plant than their respective adults. Temporal distributions of both species were correlated to crop maturity, aphid density, planting date, and corn type, but not to nearby vegetation. The within-plant locations were correlated to crop maturity, aphid density, planting date, nearby vegetation, and the presence of conspecific coccinellids. While the distribution of each population was unique, some *C. maculata* and *H. axyridis* shared time and space, providing the potential for intra-guild predation. An encounter between *H. axyridis* and *C. maculata* was most likely to occur when the corn had high aphid populations during pollen shed. These extra-guild food sources minimize intra-guild predation, allowing these two species to co-exist in New York corn and sweet corn fields.

KEY WORDS *Coleomegilla maculata*, *Harmonia axyridis*, sweet corn, intra-guild predation, distribution

PAST SURVEYS IN NEW YORK corn and sweet corn fields have found that the primary natural enemy in the region is the native predaceous coccinellid *Coleomegilla maculata* (DeGeer) (Whitman 1975, Andow and Risch 1985, Hoffmann et al. 1997). However, the recent arrival of *Harmonia axyridis* (Pallas) (Coderre et al. 1995, Wheeler and Stoops 1996) introduced a new predator into the system. This alteration of the predator guild in corn and sweet corn could have several ramifications. If *H. axyridis* supplements the existing guild, biological pest control could be increased. However, introduced coccinellids have been documented to sometimes reduce populations of native coccinellids in agricultural systems (Elliott et al. 1996), which would lead to an unknown change in biological pest control. This study was undertaken to improve our understanding of the factors that impact coccinellid populations, and thus be able to estimate the impact of *H. axyridis* on the existing coccinellid populations, with the long range goal of predicting biological control levels in corn.

Previous studies have shown that numerous factors influence coccinellid population dynamics and behavior. Coccinellid populations fluctuate over time of year, and different species can have different cycles (Hoffmann et al. 1997, Wells and McPherson 1999). The biotic factor of aphid density was examined because it has proven to be important in determining some coccinellid populations and behavior (Banks 1956, Wright and Laing 1980, Coderre et al. 1987). Corn maturity, especially pollen shed, is another biotic factor shown to influence some coccinellids (Smith 1971, Schellhorn and Andow 1999). Although field corn and sweet corn occur within the same landscape in many regions and have the same pests and natural enemies, few studies have compared predator densities in these crops (Udayagiri et al. 1997). In addition, vegetation growing adjacent to the fields can influence coccinellid populations and behavior by providing food and shelter (Harmon et al. 2000, Griffin and Yeagan 2002) and by altering the light intensity in the edge of the field (Ewert and Chiang 1966). The presence of a predator has also been shown to alter the behavior of potential prey (Beckerman et al. 1997). To

¹ E-mail: frm1@cornell.edu.

understand the intensity of the interaction between *C. maculata* and *H. axyridis* and which of the above factors influence the dynamics of these species, the temporal and within-plant location of coccinellids in corn and sweet corn fields were monitored for 3 yr.

There is concern that *H. axyridis* will have a negative impact on native coccinellids, particularly *C. maculata*. This is largely based on a laboratory study by Cottrell and Yeorgan (1998) that found *H. axyridis* larvae ate *C. maculata* larvae of the same instar $\approx 90\%$ of the time, but *C. maculata* larvae never ate *H. axyridis* larvae of the same instar. Even when a fourth-instar *C. maculata* was paired with a third-instar *H. axyridis*, *C. maculata* was still the victim 16% of the time while only feeding on *H. axyridis* 3% of the time. Only when *C. maculata* larvae were substantially larger than *H. axyridis* larvae did *C. maculata* become the predator. The authors also found that *H. axyridis* larvae can complete development on *C. maculata* eggs. Therefore, it can be concluded that when intra-guild predation occurs between these two species, *H. axyridis* will generally be the predator and *C. maculata* the prey. Furthermore, if the frequency of encounters between these coccinellids is high, the size of the *C. maculata* population is likely to decrease over time (Polis et al. 1989). General analytical models predict this would decrease total biological control from coccinellids (Rosenheim et al. 1995), although it is important to note that these models assume that the predators compete for a single food resource which is not true for *C. maculata* and *H. axyridis* in corn.

The intensity of intra-guild predation in the field is not only a function of the ability of one predator to consume a conspecific predator, but also the likelihood of encountering that species when the predator is hungry. The likelihood of encounter is a function of temporal and spatial dynamics, while the hunger of a predator is primarily a function of the availability of extra-guild food (Lucas et al. 1998, Obrycki et al. 1998, Kajita et al. 2000). In corn, extra-guild food sources are primarily aphids and corn pollen. Therefore, by knowing when pollen and aphids are abundant, the likelihood of *H. axyridis* being hungry can be estimated. By combining spatial and temporal dynamics with extra-guild food availability, the likelihood of intra-guild predation can be estimated. This study examines these factors for adults and larvae of both species. Whereas *C. maculata* adults are not vulnerable to intra-guild predation, their eggs are. Therefore, by monitoring the adults and larvae, we can project the risk of intra-guild predation for both *C. maculata* eggs and larvae.

Materials and Methods

The temporal distributions of coccinellids and aphids were recorded in weekly monitoring from 1999 to 2001. In 1999 and 2001, the within-plant distribution was also recorded during weekly monitoring. The methods used each year were slightly different, but the data obtained were analyzed similarly each year.

1999

Coccinellids and aphids were monitored weekly from mid-June until mid-September in 47 sites on 13 commercial fields in Ontario and Yates counties, NY, and four research plots at Cornell's Vegetable Research Farm in Geneva, NY. Commercial fields (five early-season sweet corn, four late-season sweet corn, and four early-season field corn) were a minimum of 5 ha in size, and the research plots (one sweet corn plot planted every 2 wk beginning in mid-May) were each 500 m². The early sweet corn and field corn was planted in mid-May, and the late sweet corn was planted in mid to late June. All sweet corn commercial fields and research plots were planted with the variety "Bonus," and several varieties of field corn were planted. A sampling site was an area of 30 m² within a field. Field count sampling began when the plants were 30 cm tall and continued weekly until the sweet corn was harvested or the field corn kernels began to dry. In commercial fields, visual counts were conducted in three sites per field, while two sites per plot were selected on the research farm. Two of the sites in each commercial field were ≈ 6 m from the edge of the field and the third site was at least 50 m from the nearest field edge. The field counts consisted of a nondestructive visual examination of 25 consecutive plants at a site. Aphids and all species of coccinellids were counted and recorded in the field as being on the top third, middle third, or lower third of the plant. Adult and second to fourth instar coccinellids were identified according to their distinct markings. First instars were classified as *H. axyridis* when the color was black and *C. maculata* when the color was gray. Rearing of some of the first instars confirmed that the field identification was accurate. Crop maturity was also recorded at each site. When early-planted corn plants were 65 cm and again during early pollen shed, 25 plants per site were taken to the laboratory for a more thorough insect count. A corn plant was cut at the soil surface and quickly placed in a large plastic bag, taking care not to dislodge the insects from the plant. The plants were frozen to kill the insects and then examined in the laboratory to identify and count all insects. The field and laboratory counts of aphids were later compared, and the weekly field-count aphid populations were adjusted to the laboratory estimates, as described below. A minimum of 50 aphids per two plants was chosen as a level needed to consider aphids present in the field. This size represents an aphid colony large enough or present for enough time that a coccinellid would likely encounter it.

2000

Sweet corn plots, each 150 m² in size, were planted with the variety "Temptation" at Cornell's Vegetable Research Farm in Geneva, NY, in late May, mid-June, and late June with three replications. Plots were monitored weekly from when the corn reached 30 cm in height until it was ready for harvest. Based on our experience in 1999, where we saw that coccinellid

populations were not very aggregated and that aphid populations varied greatly from week to week, we conducted weekly field counts by visually examining 10 plants per plot and weekly laboratory counts of two bagged plants per plot. Within-plant location was not recorded. In addition to the plots noted above, we also sampled in a nearby field that contained a sweet corn variety trial with three replications of 13 varieties planted in 28-m² plots on 31 May. These plots were monitored weekly from 5 July until harvest using the 10-plant field and two-plant laboratory count methods described above. There were no significant variety impacts on the coccinellid populations, although varieties were marginally significant for several populations (*C. maculata* adults $F = 0.41$; $df = 11, 289$; $P = 0.9530$; *C. maculata* larvae $F = 1.66$; $df = 11, 289$; $P = 0.0817$; *H. axyridis* adults $F = 1.64$; $df = 11, 289$; $P = 0.0875$; *H. axyridis* larvae $F = 1.60$; $df = 11, 289$; $P = 0.0987$). To account for this variance in the populations, the data from the variety trial were used with variety included as a random factor in the analysis.

2001

Sweet corn was planted with the variety "Candy Corner" in single blocks of 465 m² weekly from 10 May until 6 July (eight planting dates) at the Cornell Vegetable Research Farm in Geneva, NY. Weekly 10-plant field counts and 2-plant laboratory counts were conducted as in 2000 from the time the tassel could be felt in the whorl until harvest. The within-plant location of the insects was recorded in the field counts, as done in 1999. Also, weekly 10-plant field counts and 2-plant laboratory counts from the unsprayed treatments of an insecticide trial (plot size 32.5 m², variety "Prime Plus") on the same farm were used in the temporal distribution analysis. The within-plant location was not recorded in the insecticide trial; therefore, these data are not used in the within-plant distribution analysis.

Factor Codes

Factors analyzed for their impact on the temporal or within-plant distribution of the coccinellids were coded as shown in Table 1. In 1999, the field count per 25 plants was found to be equivalent to the laboratory count per two plants for aphids, so the aphid codes are equivalent for all 3 yr. Conspecific adults, larvae, or either refers to the presence of the other coccinellid species on the same field sample. Planting dates coded as "Early" include all corn planted from the end of April until the end of May. "Late" plantings include all corn planted in June and the beginning of July. Vegetation describes the plants that were growing adjacent to the monitored site. "Herbaceous" means that the field border was grass, weeds, alfalfa, or an annual crop other than corn. "Woods" describes a mature stand of trees with minimal undergrowth bordering the field. "Corn" means that the site was in the interior of the field or bordered another corn field. Field sites

Table 1. Categories for factors used in analysis of weekly monitoring data

Factor	Levels
Aphid	1999: Few: 0–50 aphids per 25 plant sample by field count Many: >50 aphids per 25 plant sample by field count 2000, 2001: Few: 0–50 aphids per 2 plant sample by lab count Many: >50 aphids per 2 plant sample by lab count
Conspecific adult, larvae, or either	1: present in field count sample 2: absent in field count sample
Corn type	1: Sweet 2: Field
Crop maturity	Vegetative: 30 cm tall until tassel felt in corn whorl Tassel: tassel in whorl until first pollen shed Pollen: first pollen shed until ear kernels have some 'milk' Milk: some 'milk' in corn kernels until harvest or kernels begin to dry
Nearby vegetation	1: Herbaceous 2: Woods 3: Corn
Planting date	1: Early 2: Late
Within-plant location	1: Lower third of plant 2: Middle third of plant 3: Top third of plant

were chosen so that nearby vegetation fit clearly into one of these categories.

Data Analysis

Weekly monitoring data for the populations of *C. maculata* adults, *C. maculata* larvae, *H. axyridis* adults, and *H. axyridis* larvae were analyzed with SAS, using PROC MIXED and PROC FREQ (SAS Institute 1999). Significance was determined using $\alpha = 0.05$. In the temporal distribution factor analysis, the commercial or research fields and varieties were random and all the coded factors were fixed. Each year was analyzed separately. In 1999, aphid density, crop maturity, planting date, nearby vegetation, and crop type were evaluated. In 2000 and 2001, corn type was not included in the analysis because only sweet corn was monitored. For the within-plant analysis, the coded numbers (1 = lower third of plant, etc.) were used to calculate a mean plant location for each population and to analyze the impact of the factors monitored. Factors analyzed were aphid density, crop maturity, planting date, nearby vegetation, corn type, conspecific adults, conspecific larvae, and conspecific adults or larvae. Data from 1999 and 2001 were analyzed together with year being a random factor. This was done after preliminary analysis showed no significant interactions involving "year" as a fixed factor. For both the temporal and within-plant analyses, least square means (LSMEANS) were calculated to estimate the value of each level of the fixed factors. To account for any correlation between these factors, type-three sums of squares were used to determine the significance of each factor. Therefore, these analyses provide conservative estimates of the association of each factor with the coccinellid population. Models were built by starting with the most significant single factor

Table 2. Mean \pm SEM coccinellid populations from weekly visual counts in sweet corn from whorl to milk stage (Geneva, NY)

Coccinellid	1999	2000	2001
	Number/100 plants	Number/100 plants	Number/100 plants
<i>C. maculata</i>			
Adults	4.2 \pm 0.5	6.1 \pm 0.8	8.0 \pm 1.0
Larvae	6.4 \pm 0.9	31.6 \pm 2.8	19.5 \pm 1.9
<i>H. axyridis</i>			
Adults	3.4 \pm 0.5	3.2 \pm 0.6	4.9 \pm 0.9
Larvae	7.3 \pm 2.5	14.5 \pm 2.3	22.3 \pm 7.0
<i>C. septempunctata</i>	0.2 \pm 0.1	0.0 \pm 0.0	1.5 \pm 0.4
<i>Hippodamia</i> spp.	0.2 \pm 0.1	0.4 \pm 0.1	1.7 \pm 0.6
<i>P. quatuordecimpunctata</i>	0.1 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0

3,800, 2,100, and 1,100 plants were sampled in 1999, 2000, and 2001, respectively. Sampling conducted weekly from July until mid-September each year.

and then adding the next most significant factors sequentially. Two-way and three-way interactions were tested after their corresponding factors had been added to the models. Factors were only added if their probability of being random was <0.05 .

A logistic procedure (PROC LOGISTIC) was used to determine the significance of pollen and aphids on the likelihood of interaction between the coccinellid species. Both pollen and aphids were coded as present or absent for each field count sample, and the proportions of samples with both species present to the total samples counted for the pollen and aphid conditions were analyzed.

Results

Coleomegilla maculata and *H. axyridis* were the only abundant coccinellids found in corn fields of western New York in 1999, 2000, and 2001, comprising $>94\%$ of the total coccinellid population each year (Table 2). These two species were also the only species to regularly lay eggs in sweet corn, as evidenced by the larval populations. Only one *Coccinella septempunctata* L. larva was found, and all the *Hippodamia* spp. and *Propylea quatuordecimpunctata* L. observed were adults.

The temporal distributions for *C. maculata*, *H. axyridis*, and aphids, primarily the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), show that *C. maculata* adult populations consistently were most numerous in late July, whereas *H. axyridis* adult populations tended to increase as the season progressed (Fig. 1). However, the two larval populations followed similar temporal patterns, especially in 2000 and 2001. The significant positive correlation coefficients (Table 3) confirm that the larval density of both species tended to follow

the same trends in 2000 and 2001. The only other significant correlations between coccinellid populations were between *H. axyridis* adults and both *C. maculata* populations in 2000. Because these correlations were not significant the other 2 yr, this may not have a strong ecological basis.

An analysis of the within-plant distributions of the coccinellids (Fig. 2) shows that a higher proportion of *C. maculata* adults and larvae occurred lower on the plant than *H. axyridis* adults and larvae (1999: $F = 90.19$; $df = 1, 1,130$; $P < 0.0001$; 2001: $F = 15.92$; $df = 1, 227$; $P < 0.0001$) and that larvae of both species occurred lower on the plant than their respective adults (1999: $F = 44.86$; $df = 1, 1,130$; $P < 0.0001$; 2001: $F = 3.67$; $df = 1, 227$; $P = 0.0566$). Others have also noted that *C. maculata* occurs lower on the plant than other coccinellids (Ewert and Chiang 1966, Wagner and Ruesink 1982, Coderre and Tourneur 1984).

Temporal Distribution Factors

Five factors (aphid density, crop maturity, planting date, nearby vegetation, and corn type) were analyzed from the 1999 data. The 2000 and 2001 data were used to evaluate the factors of aphid density, crop maturity, and planting date. Table 4 lists the significant factors, interactions, and the statistical values for each from type 3 sums of squares. Nearby vegetation was not found to be a significant factor for any population. All the other factors were significant for at least one coccinellid population in each year tested. The following text explains the statistics found in Table 4 for each population.

C. maculata Adults. No factor was correlated with the *C. maculata* adult populations in 2001, but all the factors were significant in 1999 or 2000. Because there

Table 3. Pearson correlation coefficients between temporal distribution of *C. maculata* and *H. axyridis* population densities in corn and sweet corn, Ontario and Yates counties, NY, 1999–2001

	<i>H. axyridis</i> adults						<i>H. axyridis</i> larvae					
	1999		2000		2001		1999		2000		2001	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
<i>C. maculata</i> adults	−0.034	0.537	0.188	<0.001	−0.154	0.107	−0.082	0.131	−0.062	0.231	−0.130	0.176
<i>C. maculata</i> larvae	−0.039	0.472	0.122	0.017	0.138	0.151	0.096	0.076	0.421	<0.001	0.355	<0.001

n = 340, 378, and 110 in 1999, 2000, and 2001, respectively.

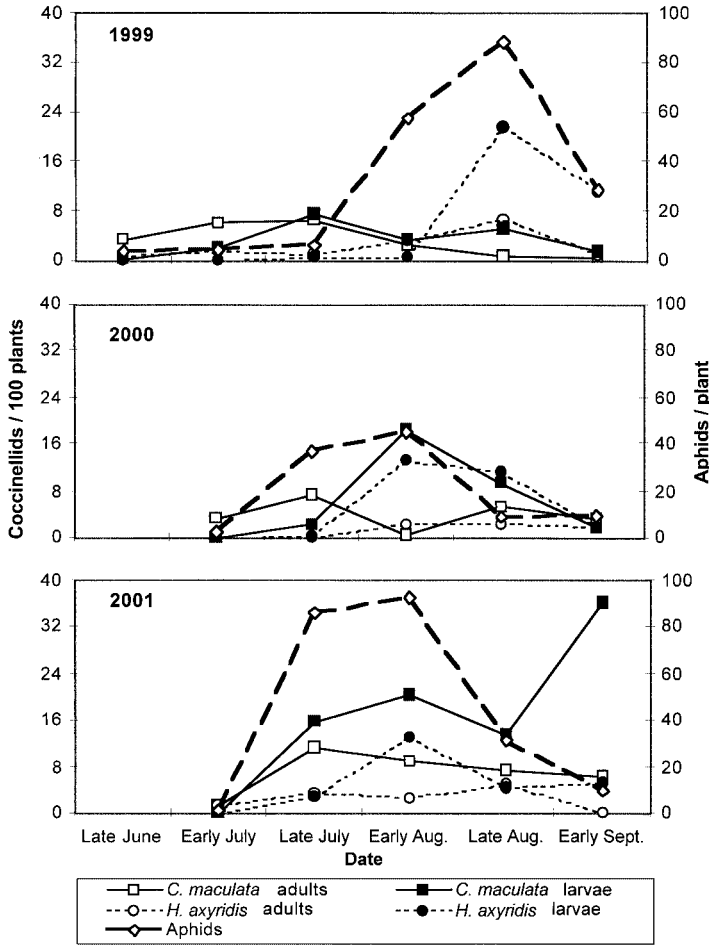


Fig. 1. Coccinellid and aphid populations over time in sweet corn, 1999–2001, Ontario and Yates Co., NY.

was no consistency over years, no conclusions can be drawn about the impact of these factors on this population. The *C. maculata* adult population was larger in the early planting, in field corn, and in tassel and pollen-stage corn in 1999, and when aphids were more numerous in 2000.

***C. maculata* Larvae.** Crop maturity and planting dates were consistent factors influencing populations for all 3 yr, with highest populations always occurring during the pollen stage. In comparing planting dates, the higher populations were always larger in the early-planted corn. In 2000, the planting date by maturity

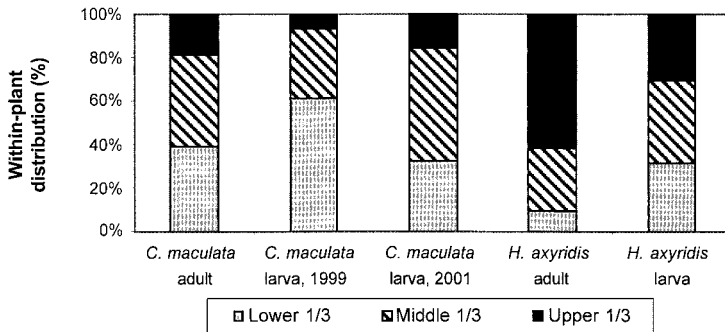


Fig. 2. Overall within-plant distribution of coccinellids in sweet corn, Ontario and Yates Co., NY, 1999 and 2001.

Table 4. Statistical values of factors (type three sums of squares) correlated to changes in the coccinellid temporal distribution from weekly monitoring corn in Ontario and Yates counties, NY, 1999–2001

Factor	<i>C. maculata</i> adult			<i>C. maculata</i> larva			<i>H. axyridis</i> adult			<i>H. axyridis</i> larva		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
1999												
Aphid density (A)			ns			ns	35.37	1,327	<0.0001	9.58	1,325	0.0021
Crop maturity (M)	14.48	3,329	<0.0001	41.24	3,330	<0.0001	3.38	3,327	0.0186	45.86	3,325	<0.0001
Planting date (P)	16.00	1,329	<0.0001	9.77	1,330	0.0019	22.26	1,327	<0.0001	43.91	1,325	<0.0001
Corn type (C)	5.93	1,329	0.0154			ns	5.98	1,327	0.0150			ns
A × P			ns			ns	19.21	1,327	<0.0001	8.91	1,325	0.0031
M × P			ns			ns			ns	32.21	3,325	<0.0001
2000												
Aphid density (A)	18.49	1,363	<0.0001			ns	8.87	1,360	0.0031			ns
Crop maturity (M)			ns	22.47	3,357	<0.0001	4.18	3,360	0.0063	56.38	3,360	<0.0001
Planting date (P)			ns	6.15	1,357	0.0136			ns	8.22	1,360	0.0044
M × P			ns	3.93	3,357	0.0088			ns			ns
2001												
Aphid density (A)			ns			ns	9.95	1,106	0.0021			ns
Crop maturity (M)			ns	24.63	2,104	<0.0001			ns	6.53	2,102	0.0021
Planting date (P)			ns	5.51	1,104	0.0208			ns	15.78	1,102	0.0001
M × P			ns			ns			ns	3.99	2,102	0.0215

Data transformed by logarithm.

ns, not significant at $\alpha = 0.05$.

Interactions that were not significant were not added to the model.

interaction was significant, with the difference between early and late plantings more pronounced during the pollen and milk stages than in the earlier stages of maturity.

***H. axyridis* Adults.** Aphid density was a major factor influencing adult populations, because many aphids were associated with larger populations each year (Fig. 3). The aphid by planting date interaction was significant in 1999 because populations responded more dramatically to high aphid density in the late-planted corn than in the early-planted corn. Crop maturity was also a significant factor in 1999 and 2000, with highest populations occurring during the tassel and pollen stages. Higher populations in the late-planted corn and in sweet corn were found in 1999.

***H. axyridis* Larvae.** While larvae were more likely to be present when aphids were plentiful every year (1999: $\chi^2 = 21.96$, *df* = 1, $P < 0.0001$; 2000: $\chi^2 = 6.67$, *df* = 1, $P = 0.0098$; 2001: $\chi^2 = 6.06$, *df* = 1, $P = 0.0139$), the factor analysis only showed aphids to be an important factor in 1999, whereas crop maturity and

planting date were influencing factors each year. Populations were highest during the pollen and milk stages each year. The impact of planting date was inconsistent, with late plantings having higher populations in 1999 when aphid populations peaked late, but early plantings having higher populations in 2000 and 2001 when aphid populations peaked earlier than in 1999. In 1999, *H. axyridis* larval populations were higher when aphid density was high, especially in the late planting when aphid populations were very high. The significant maturity by planting date interactions in 1999 and 2001 were a result of the larger populations in the one planting being more pronounced during the pollen and milk stages than during the earlier maturity stages.

Within-Plant Distribution Factors

Several factors were found to be associated with changes in the within-plant distribution for each of the coccinellid populations (Table 5; Fig. 2). No factor was significant for all the populations. Corn type was evaluated as a factor and was not significant for any of the populations. The year sampled was found to be significant only for the *C. maculata* larval population ($F = 21.69$; *df* = 1, 410; $P < 0.0001$), with the populations being lower on the plant in 1999 than in 2001. However, no interactions with year were significant; therefore, year was included in the final model as a random variable, and none of the results for the factors were separated by year. The following text explains the statistics shown in Table 5.

***C. maculata* Adults.** Adults were found higher on the plant during the vegetative stage than during the other maturity stages. They were also found higher on the plant when *H. axyridis* adults were present. This may be because of the fact that the *H. axyridis* adults were present mainly when aphids were abundant in the

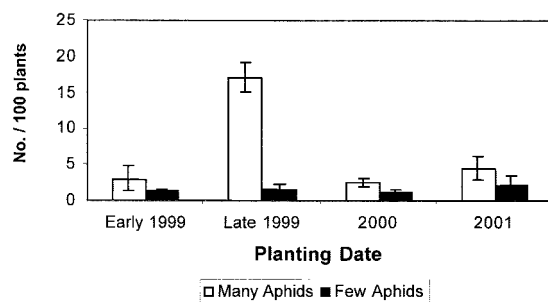


Fig. 3. *H. axyridis* adult population density (\pm SEM) as associated with aphid density each year and early and late planting dates in 1999 as estimated by least square means, 1999–2001, Ontario and Yates Co., NY.

Table 5. Statistical values of factors (type 3 sums of squares) correlated to changes in the within-plant distribution of coccinellids from weekly monitoring corn and sweet corn in Ontario and Yates Co, NY, 1999 and 2001

Factor	<i>C. maculata</i> adult			<i>C. maculata</i> larva			<i>H. axyridis</i> adult			<i>H. axyridis</i> larva		
	F	df	P	F	df	P	F	df	P	F	df	P
Aphid density			ns			ns	12.30	1,185	0.0006	6.01	1,327	0.0148
Crop maturity	7.78	3,407	<0.0001	3.49	3,450	0.0157			ns			ns
Vegetation			ns	7.80	2,450	0.0005			ns			ns
Conspecific adults	4.14	1,407	0.0424			ns	3.86	1,185	0.0509			ns
Conspecific adults or larvae			ns			ns			ns	35.95	1,327	<0.0001

ns, not significant at $\alpha = 0.05$.

Factors that were not significant were not added to the model.

tassels of the corn, so the *C. maculata* adults also climbed up the plant to feed on the aphids. However, it is important to note that the mean \pm SEM location on the plant when *H. axyridis* adults were present was 1.88 ± 0.07 , well below the mean *H. axyridis* adult location on the plant of 2.51 ± 0.18 .

***C. maculata* Larvae.** Larvae were found lower on the plant during the vegetative and tassel stages than during the pollen and milk stages. The nearby vegetation factor was significant, with larvae near herbaceous vegetation being significantly lower on the plant than when near woods or in the field interior. This may be a function of larvae avoiding the higher light intensity found in the canopy in field edges without shade.

***H. axyridis* Adults.** Because aphid populations were primarily located in the tassel, *H. axyridis* adults were found higher on the plant when aphid populations were high. When *C. maculata* adults were present, *H. axyridis* adults were found higher on the plant than when *C. maculata* adults were absent.

***H. axyridis* Larvae.** Like the *H. axyridis* adults, the larvae were found higher on the plant when aphid populations were high. In contrast to the behavior found in the adults, *H. axyridis* larvae were found lower on the plant when *C. maculata* adults or larvae were present, resulting in a higher likelihood of encounter than would be expected by examining the mean within-plant distributions of the species.

Likelihood of Intra-guild Predation

The growth stages and species partially segregated by time, but there was not complete segregation as 32% of *C. maculata* adults, and 51% of *C. maculata* larvae occurred in the same field count sample (25 plants in 1999, 10 plants in 2000 and 2001) as one or more *H. axyridis* adults or larvae. When jointly considering the temporal and within-plant segregation, only 16% of *C. maculata* adults and 25% of *C. maculata* larvae were found on the same part of the plant in the same field count as *H. axyridis* adults or larvae. The availability of extra-guild food when an encounter occurs is the other major component to be considered when predicting the intensity of intra-guild predation. Co-occurrence of the coccinellid species was mostly during the pollen maturity stage ($\chi^2 = 42.48$, $df = 1$, $P < 0.0001$) or when aphid densities were high ($\chi^2 =$

9.03, $df = 1$, $P = 0.0027$). The pollen by aphid interaction was not significant in predicting when the coccinellids would co-occur ($\chi^2 = 0.02$, $df = 1$, $P = 0.9023$). In 1999 and 2001, 12% of the *C. maculata* adults and 10% of the *C. maculata* larvae monitored co-occurred in time with *H. axyridis* when extra-guild food was scarce. If time, space, and extra-guild food factors are examined together, only 5% of the *C. maculata* larvae and eggs from 6% of the *C. maculata* adults are at high risk of being prey for *H. axyridis*. In these samples where both species occurred and extra-guild food was scarce, the *C. maculata* outnumbered the *H. axyridis* three to one. This low *H. axyridis* density, combined with the fact that *H. axyridis* adults use short-distance cues to find prey (Harmon et al. 1998) and larvae find prey primarily by direct contact with prey or prey tracks (Ferran et al. 1997), make it likely that even some proportion of these *C. maculata* were able to avoid predation.

Discussion

Harmonia axyridis and *C. maculata* were the only abundant coccinellids found in corn and sweet corn fields of western New York in 1999, 2000, and 2001. *C. maculata* adults were most numerous during July and mainly lived in the lower two-thirds of the plant, whereas *H. axyridis* adults were most numerous in August and mainly lived in the upper one-third of the plant. There was less segregation in time and space between the larval populations, so intra-guild predation and competition for food between the larvae of the two species could be expected. Planting date, crop maturity, aphid density, nearby vegetation, and corn type were all factors that influenced coccinellid population dynamics. These factors influenced the populations differently. At times, there was a very low likelihood of the two species encountering each other because of distinct temporal and spatial dynamics. The highest rate of co-occurrence was when aphid densities were high in pollen-stage corn and sweet corn.

The potential impact of *H. axyridis* on the native *C. maculata* when they co-occur can be from competition for food or through intra-guild predation (Cottrell and Yeargan 1998). Competition could play a role if *H. axyridis* out-competed *C. maculata* for a common food resource as occurs between *C. maculata* and *C. septempunctata* (Obrycki et al. 1998). While *H. axyri-*

dis is more aggressive in competing for food (Cottrell and Yeargan 1998), *C. maculata* tends to be more polyphagous (Putnam 1964), so it is able to use food resources such as pollen that *H. axyridis* is less able to use. Because the coccinellids are not directly competing for all their food resources, the direct impact of food competition on the population of either species is likely minimal.

The more substantial threat from *H. axyridis* may be that it will reduce *C. maculata* populations through intra-guild predation. This requires that the species encounter each other and that the intra-guild predator be hungry. Based on these 3 yr of data, the highest encounter rate between *C. maculata* adults and larvae and *H. axyridis* adults and larvae will be when the corn has high aphid populations in pollen-stage corn. Because these are both food resources, the highest rate of intra-guild predation may not be during these high encounter periods, but somewhat later, when coccinellid populations are still fairly large, the larvae are mostly late instars with a large appetite, and the aphid and pollen food resources are shrinking. In corn and sweet corn, this vulnerable period only represents 5% of the *C. maculata* larvae and 6% of the eggs laid by adults, levels that are probably not significant given the high rate of mortality from all factors (Obrycki et al. 1997). While the data indicate that the intensity of intra-guild predation between *C. maculata* larvae and *H. axyridis* should be minimal in corn and sweet corn, it was occasionally observed during monitoring, and *H. axyridis* adults and larvae were eating *C. maculata* larvae and not vice versa (F.R.M., unpublished data.).

There is no evidence that *C. maculata* modify their behavior to avoid encounters with *H. axyridis*. The presence of *H. axyridis* adults resulted in no change in the within-plant distribution of *C. maculata* larvae, and *C. maculata* adults were found higher on the plant, closer to where *H. axyridis* adults and larvae were found. Interestingly, both *H. axyridis* adults and larvae had different within-plant distributions when *C. maculata* were present. *Harmonia axyridis* adults moved higher on the plant, further away from *C. maculata* adults, while *H. axyridis* larvae moved lower, increasing the potential rate of encounter with *C. maculata*. Whether these changes in distribution are a direct result of the presence of the other predator or a function of some other variables not measured can only be determined by conducting more controlled experiments.

Both coccinellids are common in corn and sweet corn, but intra-guild predation by *H. axyridis* is not expected to severely impact *C. maculata* in these habitats. However, these are not the only habitats for either of these coccinellids. Both species can also be found on some other agricultural plants where the temporal, spatial, and extra-guild food factors may have very different impacts on coccinellid dynamics. As a result, intra-guild predation intensity may be higher in some habitats than found in this study. Both species also have unique habitats. *C. maculata* is common in alfalfa but not in trees (Colunga-Garcia et al. 1997), whereas *H. axyridis* is common in many arbo-

real habitats but rare in alfalfa (LaMana and Miller 1996). To predict the overall impact of *H. axyridis* on *C. maculata* would require an extensive landscape approach. This current study, however, shows that intra-guild predation within New York corn and sweet corn fields, which comprise 23% of the cropland in New York (NYASS 2002), should not be an environment where intra-guild predation is severe. As a result, there is a reasonable likelihood that both *C. maculata* and *H. axyridis* will be able to co-exist in the corn and sweet corn ecosystems, providing as much or more biological pest control as before the arrival of *H. axyridis*.

Acknowledgments

We thank J. Allen, R. S. Boyd, Jr., P. Smereka, M. Musser, and S. Millis for assistance with data collection. We also thank B. Nault, M. Hoffmann, J. Nyrop, and two anonymous reviewers for suggestions in revising earlier drafts of this manuscript. Partial funding for this project was provided by the Paul Chapman Fellowship from the Department of Entomology at NYSAES and the New York State Integrated Pest Management Program.

References Cited

- Andow, D. A., and S. J. Risch. 1985. Predation in diversified agroecosystems: relations between a coccinellid predator *Coleomegilla maculata* and its food. *J. Appl. Ecol.* 22: 357–372.
- Banks, C. J. 1956. The distribution of coccinellid egg batches and larvae in relation to numbers of *Aphis fabae* Scop. on *Vicia faba*. *Bull. Entomol. Res.* 47: 47–56.
- Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proc. Nat. Acad. Sci. USA* 94: 10735–10738.
- Coderre, D., E. Lucas, and I. Gagne. 1995. The occurrence of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in Canada. *Can. Entomol.* 127: 609–611.
- Coderre, D., L. Provencher, and J. C. Tourneur. 1987. Oviposition and niche partitioning in aphidophagous insects on maize. *Can. Entomol.* 119: 195–203.
- Coderre, D., and J. C. Tourneur. 1984. Vertical distribution of aphids and aphidophagous insects on maize, pp. 291–296. *In* I. Hodek (ed.), *Ecology of aphidophaga*, *Zvukovske Podhradi*. Dr W Junk Publishers, Dordrecht.
- Colunga-Garcia, M., S. H. Gage, and D. A. Landis. 1997. Response of an assemblage of coccinellidae (Coleoptera) to a diverse agricultural landscape. *Environ. Entomol.* 26: 797–804.
- Cottrell, T. E., and K. V. Yeargan. 1998. Intra-guild predation between an introduced lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). *J. Kans. Entomol. Soc.* 71: 159–163.
- Elliott, N., R. Kieckhefer, and W. Kauffman. 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia (Berl.)* 105: 537–544.
- Ewert, M. A., and H. C. Chiang. 1966. Effects of some environmental factors on the distribution of three species of Coccinellidae in their microhabitat, pp. 195–219. *In* I. Hodek (ed.), *Ecology of aphidophagous insects*, Liblice. Academia, Prague.

- Ferran, A., J. Gambier, S. Parent, K. Legendre, R. Tourniere, and L. Giuge. 1997. The effect of rearing the ladybird *Harmonia axyridis* on *Ephesthia kuehniella* eggs on the response of its larvae to aphid tracks. *J. Insect Behav.* 10: 129–144.
- Griffin, M. L., and K. V. Yeorgan. 2002. Factors potentially affecting oviposition site selection by the lady beetle *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Environ. Entomol.* 31: 112–119.
- Harmon, J. P., A. R. Ives, J. E. Losey, A. C. Olson, and K. S. Rauwald. 2000. *Coleomegilla maculata* (Coleoptera: Coccinellidae) predation on pea aphids promoted by proximity to dandelions. *Oecologia (Berl.)* 125: 543–548.
- Harmon, J. P., J. E. Losey, and A. R. Ives. 1998. The role of vision and color in the close proximity foraging behavior of four coccinellid species. *Oecologia (Berl.)* 115: 287–292.
- Hoffmann, M. P., M. S. Orfanedes, L. H. Pedersen, J. J. Kirkwyland, E. R. Hoebeke, and R. Ayyappath. 1997. Survey of lady beetles (Coleoptera: Coccinellidae) in sweet corn using yellow sticky cards. *J. Entomol. Sci.* 32: 358–369.
- Kajita, Y., F. Takano, H. Yasuda, and B. K. Agarwala. 2000. Effects of indigenous ladybird species (Coleoptera: Coccinellidae) on the survival of an exotic species in relation to prey abundance. *Appl. Entomol. Zool.* 35: 473–479.
- LaMana, M. L., and J. C. Miller. 1996. Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. *Biol. Control.* 6: 232–237.
- Lucas, E., D. Coderre, and J. Brodeur. 1998. Intra-guild predation among aphid predators: characterization and influence of extraguild prey density. *Ecology* 79: 1084–1092.
- [NYASS] New York Agricultural Statistics Service. 2002. New York agricultural statistics 2001–2002. New York Agricultural Statistics Service, Albany, NY.
- Obrycki, J. J., K. L. Giles, and A. M. Ormord. 1998. Interactions between an introduced and indigenous coccinellid species at different prey densities. *Oecologia (Berl.)* 117: 279–285.
- Obrycki, J. J., A. M. Ormord, and K. L. Giles. 1997. Partial life table analysis for larval *Coleomegilla maculata* (Degeer) and *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) in alfalfa. *J. Kans. Entomol. Soc.* 70: 339–346.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intra-guild predation: potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* 20: 297–330.
- Putnam, W. L. 1964. Occurrence and food of some coccinellids (Coleoptera) in Ontario peach orchards. *Can. Entomol.* 96: 1149–1155.
- Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marois, and B. A. Jaffee. 1995. Intra-guild predation among biological-control agents: theory and evidence. *Biol. Control.* 5: 303–335.
- SAS Institute. 1999. SAS/STAT user's guide, version 8. SAS Institute, Cary, NC.
- Schellhorn, N. A., and D. A. Andow. 1999. Mortality of coccinellid (Coleoptera: Coccinellidae) larvae and pupae when prey become scarce. *Environ. Entomol.* 28: 1092–1100.
- Smith, B. C. 1971. Effects of various factors on the local distribution and density of coccinellid adults on corn (Coleoptera: Coccinellidae). *Can. Entomol.* 103: 1115–1120.
- Udayagiri, S., C. E. Mason, and J. D. Pesek, Jr. 1997. *Coleomegilla maculata*, *Coccinella septempunctata* (Coleoptera: Coccinellidae), *Chrysoperla carnea* (Neuroptera: Chrysopidae), and *Macrocentrus grandii* (Hymenoptera: Braconidae) trapped on colored sticky traps in corn habitats. *Environ. Entomol.* 26: 983–988.
- Wagner, S. W., and W. G. Ruesink. 1982. The distribution of natural enemies of the corn leaf aphid, *Rhopalosiphum maidis* [Homoptera: Aphididae] on field corn. *Gt. Lakes Entomol.* 15: 153–157.
- Wells, M. L., and R. M. McPherson. 1999. Population dynamics of three coccinellids in flue-cured tobacco and functional response of *Hippodamia convergens* (Coleoptera: Coccinellidae) feeding on tobacco aphids (Homoptera: Aphididae). *Environ. Entomol.* 28: 768–773.
- Wheeler, A. G., Jr., and C. A. Stoops. 1996. Status and spread of the Palearctic lady beetles *Hippodamia variegata* and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in Pennsylvania, 1993–1995. *Entomol. News.* 107: 291–298.
- Whitman, R. J. 1975. Natural control of European corn borer, *Ostrinia nubilalis* (Hübner) in New York. Ph.D. dissertation, Cornell University, Ithaca, NY.
- Wright, E. J., and J. E. Laing. 1980. Numerical response of coccinellids to aphids in corn in southern Ontario. *Can. Entomol.* 112: 977–988.

Received for publication 26 September 2002; accepted 26 March 2003.